

Effects of temperature and photoperiod on predation attributes and development of two *Coccinella* species (Coleoptera: Coccinellidae)

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Abstract: 【Aim】 In agriculture, climatic changes affect crop yield, dynamics of aphid pests and their regulation by ladybird predators. While some ladybirds are ubiquitous and others have limited geographical ranges; but how climatic cues influence distribution of ladybirds is poorly explored. 【Methods】 Present study, therefore, assesses the effects of different temperatures (15°C, 20°C, 25°C, 30°C and 35°C), and photoperiods (8L:16D, 12L:12D and 16L:8D) on consumption and utilization of the pea aphid, *Acyrtosiphon pisum* (Harris) by larvae of a ubiquitous ladybird [*Coccinella septempunctata* (Linnaeus)] and an Oriental/south-Asian ladybird (*Coccinella transversalis* Fabricius). 【Results】 Although predation attributes and developmental rates of both ladybirds were the highest at 25°C and attributes further increased with increase in day length (from 8L:16D to 16L:8D photoperiod), larvae of *C. septempunctata* had higher consumption, growth and developmental rates, and their newly emerged adults were heavier than those of *C. transversalis* at all temperatures and photoperiods. Non-linear regression model extrapolated ~11°C and ~10.5°C as lower development thresholds and ~41°C and ~43°C as upper development thresholds for *C. transversalis* and *C. septempunctata*, respectively. Dependency of larval predation and developmental rates to climatic cues were higher in *C. transversalis* than *C. septempunctata*. 【Conclusion】 Present study, therefore, reveals that a ubiquitous ladybird is less susceptible to climatic cues than an indigenous ladybird and hence is widely distributed to different geographical regions. Thus, the former may behave as a better biocontrol agent than the latter.

Key words: *Coccinella septempunctata*; *Coccinella transversalis*; ladybirds; temperature; photoperiod; aphid

1 INTRODUCTION

Over the last 100 years, the mean air temperature of the earth has increased by about 1°C (IPCC, 2007). This global rise in temperature, leading to climatic changes, is mainly owing to annual increase in atmospheric CO₂ and tropospheric ozone (IPCC, 2007). In agriculture, climatic change affects the crop yield, dynamics of pests and their regulation by natural enemies (Selvaraj *et al.*, 2013). Studies have shown that climate change can influence the distribution of phytophagous pests (Batalden *et al.*, 2007; Trnka *et al.*, 2007) by affecting their arrival (Parmesan, 2007), emergence (Dewar and Watt, 1992) and the potential of their natural enemies (Stireman *et al.*, 2005; Abbott *et al.*, 2014).

Amongst natural enemies of pests, the ladybirds (Coleoptera: Coccinellidae) are the commonest insect predators owing to their wide prey range (Hodek *et al.*, 2012). Being poikilothermic in nature, they are highly susceptible to climatic

change, *i. e.*, variation in temperature and photoperiod (Reznik and Vaghina, 2011; Omkar *et al.*, 2008, 2009, 2013; Majumder and Agarwala, 2013; Kumar and Omkar, 2015). Ladybirds avoid low temperature extremes by migration and dispersal or by entering into diapause (Dixon, 2000; Hodek *et al.*, 2012). Also their fitness decreases at an extremely high temperature (Zhang *et al.*, 2014). Photoperiod governs the gross hormonal and gonadal changes in ladybirds necessary for the transition between developmental stages and reproductive activity (Omkar and Pathak, 2006; Hodek *et al.*, 2012). Photoperiod is often used by ladybirds as a measure of seasonal change and as a cue for activities like growth and development (Reznik *et al.*, 2015a). It guides them to differentiate among the environmental fluctuations and to synchronize their activities accordingly (Hodek *et al.*, 2012). Thus, both temperature and photoperiod influence various biological characteristics, *e. g.*, development, survival, fecundity, fertility and longevity of a ladybird species.

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While some ladybirds are ubiquitous, *e. g.*, *Coccinella septempunctata* L. and *Adalia bipunctata* (L.) (Czechowska and Bielawski, 1981; Hodek and Michaud, 2008), majority of them have limited geographical ranges, *e. g.*, *Stethorus punctillum* Ws. is Euro-Siberian; *Synharmonia impustulata* L. is European, *Adalia decempunctata* (L.) and *Scymnus bipunctatus* Kugel. are Palaearctic, and *Coccinella transversalis* Fab., *Propylea dissecta* (Mulsant) and *Menochilus sexmaculatus* (Fabr.) are Oriental species (Czechowska and Bielawski, 1981; Omkar *et al.*, 2005; Kumar and Omkar, 2015). Since a rise in temperature (Nylín and Gotthard, 1998) and/or an increase in day length (Berkvens *et al.*, 2008) promote the growth and development of ladybirds, but would the responses of climatic cues differ between a ubiquitous ladybird and a ladybird distributed to narrow geographical ranges? Would a rise in temperature and/or an increase in day length leads to a higher prey consumption and utilization by the larvae of the former than the latter or *vice versa*? Would the larvae of the former or those of the latter, develop faster with rising temperature and/or increasing photoperiod?

Moreover, in spite of numerous studies on the effect of temperature and photoperiod on predation and life attributes of individual ladybirds, the question that how temperature and photoperiodic conditions influence the distribution of ladybird species is poorly explored. The question that why certain ladybird species are ubiquitous while others are distributed to specific geographical regions is not answered in earlier studies evaluating the effects of temperature and photoperiod. Studies that assess the effects of temperature and photoperiod on the distribution of ladybirds would not only help in targeting the search for the best biocontrol agents (Ulrichs and Hopper, 2008; Lu *et al.*, 2015), but would also increase the possibility of their intentional introductions and improve risk assessment for accidental introductions.

Thus, despite assessing the effects of five different temperatures (15°C, 20°C, 25°C, 30°C and 35°C) and three different photoperiods (8L:16D, 12L:12D and 16L:8D) on the consumption, conversion and utilization of the pea aphid, *Acyrtosiphon pisum* (Harris) by larvae of *C. septempunctata* (Linnaeus) and *C. transversalis* Fabricius, the present study would try to answer the question that how climatic cues influence the distribution of ladybirds? *C. septempunctata* is a ubiquitous ladybird (Omkar and Pervez, 2002; Hodek and Michaud, 2008), while *C. transversalis*

is native to India and is found primarily in South Asia (Omkar *et al.*, 2005). Both the ladybirds are large in size and polyphagous; and within the Indian sub-continent, both co-exist as predators of numerous species of aphids that infest the agricultural crops. The findings of the present study would also be helpful in providing suggestions for optimizing the practical use of both the ladybirds in greenhouses.

2 MATERIALS AND METHODS

2.1 Maintenance of stock culture

Adults of *C. septempunctata* (n = 40) and *C. transversalis* (n = 40), collected from the fields of Lucknow (26°50'N, 80°54'E), India, were paired and reared for three generations in plastic Petri dishes (14.5 cm × 1.5 cm) under 27 ± 2°C temperature; 65% ± 5% relative humidity and 14L:10D photoperiod in BOD incubators (Yorco Super Deluxe, YSI-440, New Delhi, India). They were provided with *ad libitum* pea aphid, *A. pisum*, reared on broad bean, *Vicia faba* L. (Fabaceae) and maintained in polyhouse (22 ± 1°C, 65% ± 5% RH and 14L:10D photoperiod). Wild ladybirds from the field were frequently added to this established stock to prevent inbreeding. The eggs laid were collected every 24 h, kept in BOD incubators and observed for hatching, and the neonates obtained were used in the experiments.

The pea aphid, *A. pisum* is a pest of various leguminous hosts in the temperate zones of North America, Europe and most of Southern Asia (Harper *et al.*, 1978), that results in severe crop losses of beans and peas (de Zoeten and Skaf, 2001). It is a large, pale-green aphid; and like most aphids, it displays cyclical parthenogenesis. In summer, females are produced by parthenogenesis from diploid, unfertilized eggs. They develop to adulthood in nearly two weeks and give birth almost immediately. In fall, changing photoperiod triggers the production of sexual males and females. After mating, the sexual female lays a few large, overwintering eggs that hatches into a female nymph and serves as a fundatrix, the first individual of a new clone (Sharp and Andrade, 1994).

2.2 Effect of temperature on prey consumption and utilization

Neonates of *C. septempunctata* (n = 50) and *C. transversalis* (n = 50) were weighed 12 h after hatching using an electronic balance (Sartorius CP225-D; 0.01 mg precision). They were kept individually in Petri dishes on daily replenishment of *ad libitum* (50 mg ~ 100 3rd instar larvae) supply

of *A. pisum* in BOD incubators under one of the following temperatures (treatments): (i) $15 \pm 2^\circ\text{C}$ (low, $n = 10$ neonates per ladybird species); (ii) $20 \pm 2^\circ\text{C}$ (low, $n = 10$ neonates per ladybird species); (iii) $25 \pm 2^\circ\text{C}$ (medium, $n = 10$ neonates per ladybird species); (iv) $30 \pm 2^\circ\text{C}$ (high, $n = 10$ neonates per ladybird species), and (v) $35 \pm 2^\circ\text{C}$ (high, $n = 10$ neonates per ladybird species). Relative humidity and photoperiod were kept the same to that of stock culture. The five different temperature ranges used in present study have also been used in many earlier studies evaluating the effect of temperature in ladybirds (Aksit *et al.*, 2007; Wang *et al.*, 2013; Jarosik *et al.*, 2014; Kumar and Omkar, 2015). Moreover, preliminary investigations were undertaken to insure that: (i) all the larval stages of both the ladybird species could feed on the 3rd instar larvae of *A. pisum*; and (ii) 50 mg of the 3rd instar larvae (~ 100 individuals) was the *ad libitum* diet for all the larval stages.

The immature stages of ladybirds were reared under the respective temperatures throughout their development. Every 12 h, the immature stages of ladybirds were inspected for the presence of moults and their developmental durations were recorded accordingly. However, the stages were separated from the remaining biomass of prey every 24 h, weighed and were provided with a fresh amount of *ad libitum* prey biomass. The remaining prey biomass was also weighed every 24 h.

The 3rd instar larvae of *A. pisum* showed 15% and 30% mortality at 30°C and 35°C , respectively, under control treatments. Therefore, to assess the reduction in biomass of prey under different temperatures (especially at 30°C and 35°C) in absence of a predator (control), measured amount of prey biomass was placed individually in Petri dishes, kept under experimental abiotic conditions for 24 h and then weighed. The average loss in biomass of the prey per temperature based on 5 replicates was taken into account in the analysis of the data. Consumption rate, conversion efficiency and growth rate of larvae (per stage, *i. e.*, 1st/2nd/3rd/4th instar stage) were calculated using the following formulae (modified after Kumar *et al.*, 2014):

1. Consumption rate (mg/d) = Aphid biomass (mg) consumed by the larval stage/Developmental duration (d) of the larval stage;
2. Conversion efficiency = Increase in biomass (mg) of larval stage/Aphid biomass (mg) consumed by larval stage;
3. Growth rate ($/\text{day}$) = Fresh biomass gain (mg)

by the larval stage/[Developmental duration (d) of larval stage \times mean body mass (mg) of larval stage].

For each temperature, development rate (DR) of both the ladybird species was calculated as the reciprocal of total development period of their immature stages. The temperature dependence of the developmental rate and the developmental thresholds were established by means of both the linear and non-linear (polynomial) regression models (Kontodimas *et al.*, 2004).

2.3 Effect of photoperiod on prey consumption and utilization

The adults of *C. septempunctata* ($n = 10$) and *C. transversalis* ($n = 10$) that were obtained from the most favourable temperature of the previous experiment were paired in plastic Petri dishes on *ad libitum* (50 mg) supply of *A. pisum* under the similar abiotic conditions. Eggs laid were separated and the obtained neonates were used in the experiments.

Neonates of both the ladybirds ($n = 30$ per ladybird species) were weighed after hatching using an electronic balance (Sartorius CP225-D; 0.01 mg precision) and kept individually in Petri dishes (size as above) under one of the following photoperiod regimes: (i) 8L: 16D (short day length; $n = 10$ neonates per ladybird species), (ii) 12L: 12D (equinox; $n = 10$ neonates per ladybird species), and (iii) 16L: 8D (long day length; $n = 10$ neonates per ladybird species) in BOD incubators (at $25 \pm 2^\circ\text{C}$ temperature, $65\% \pm 5\%$ relative humidity) on *ad libitum* diet (50 mg) of *A. pisum*. The immature stages of ladybirds were maintained under these photoperiods throughout their development. Every 24 h, the immature stages of ladybirds were separated from the remaining prey biomass, weighed and were provided with a fresh amount of *ad libitum* prey biomass. The prey remnants were also weighed every 24 h. However, the immature stages of ladybirds were inspected for the presence of larval moults every 12 h and their developmental durations were recorded accordingly.

To assess the reduction in biomass of prey in absence of a predator (control), measured amounts of prey biomass was placed individually in Petri dishes, kept under the experimental abiotic conditions for 24 h and then weighed. The average loss in prey biomass per photoperiodic condition, if any, based on five replicates was taken into account in the analysis of the data. Consumption rate, conversion efficiency, growth rate and developmental rate of larvae (per stage) were calculated using the

above mentioned formulae.

2.4 Statistical analysis

The data on consumption rate, conversion efficiency and growth rate were checked for normal distribution using Kolmogorov-Smirnoff test for normality and Bartlett’s test for homogeneity of variances prior to analysis. Consumption rate, conversion efficiency and growth rate (dependent factors), were individually subjected to multivariate analysis of variance (MANOVA) followed by Tukey’s *post hoc* comparison of means, considering ladybird species, larval stage, temperature/photoperiod and their interactions as the independent factors. Regression coefficients of each larval stage per ladybird species between: (i) temperature/photoperiod and consumption rate, (ii) temperature/photoperiod and conversion efficiency, and (iii) temperature/photoperiod and growth rate, were further calculated.

However, mean body mass of newly emerged adults and developmental rate of ladybirds at the immature stages (dependent factors) were individually subjected to MANOVA treating ladybird species, temperature/photoperiod and their interaction as independent factors. Mean body

biomass and developmental rate of both the ladybird species were further regressed against different temperatures. All statistical analyses were performed on MINITAB 16 (Minitab Inc., State College, Pennsylvania, USA).

3 RESULTS

3.1 Effect of temperature on predation and development of the immature stages of the two *Coccinella* species

The ladybird species, temperature and larval stage had significant influence on the consumption rate of larval instars. Except the interaction between ladybird species and temperature which was significant, the other interactions between the independent factors were insignificant (Table 1). The consumption rate of most of the larval stages increased from 15 to 25°C , and thereafter decreased from 25 to 35°C ; being the highest at 25°C . At all temperatures, the 4th instar larvae of both the ladybirds had higher consumption rate than early instars; and *C. septempunctata* had higher consumption rates than *C. transversalis* (Table 2 ; Fig. 1).

Table 1 MANOVA table showing the effects of independent variables on dependent variables, viz., consumption rate, conversion efficiency and growth rate of larval instars of *Coccinella septempunctata* and *Coccinella transversalis*

Independent variables	Temperature		
	Consumption rate	Conversion efficiency	Growth rate
Ladybird species	$F = 21.97; P < 0.0001; df = 1, 399$	$F = 483.79; P < 0.0001; df = 1, 399$	$F = 340.82; P < 0.0001; df = 1, 399$
Temperature	$F = 18.72; P < 0.0001; df = 4, 399$	$F = 136.41; P < 0.0001; df = 3, 399$	$F = 44.60; P < 0.0001; df = 4, 399$
Larval stage	$F = 48.03; P < 0.0001; df = 3, 399$	$F = 43.47; P < 0.0001; df = 4, 399$	$F = 1209.61; P < 0.0001; df = 3, 399$
Ladybird species × temperature	$F = 3.40; P = 0.010; df = 4, 399$	$F = 15.07; P < 0.0001; df = 4, 399$	$F = 35.12; P < 0.0001; df = 4, 399$
Ladybird species × larval stage	$F = 0.84; P = 0.473; df = 3, 399$	$F = 151.44; P < 0.0001; df = 3, 399$	$F = 52.98; P < 0.0001; df = 3, 399$
Temperature × larval stage	$F = 1.66; P = 0.074; df = 12, 399$	$F = 3.04; P < 0.0001; df = 12, 399$	$F = 1.40; P = 0.165; df = 12, 399$
Ladybird species × temperature × larval stage	$F = 1.27; P = 0.231; df = 12, 399$	$F = 2.83; P = 0.001; df = 12, 399$	$F = 4.62; P < 0.0001; df = 12, 399$

Independent variables	Photoperiod		
	Consumption rate	Conversion efficiency	Growth rate
Ladybird species	$F = 47.71; P < 0.0001; df = 1, 239$	$F = 87.74; P < 0.0001; df = 1, 239$	$F = 22.55; P < 0.0001; df = 1, 239$
Photoperiod	$F = 62.33; P < 0.0001; df = 2, 239$	$F = 46.71; P < 0.0001; df = 2, 239$	$F = 141.24; P < 0.0001; df = 2, 239$
Larval stage	$F = 60.63; P < 0.0001; df = 3, 239$	$F = 39.27; P < 0.0001; df = 3, 239$	$F = 150.67; P < 0.0001; df = 3, 239$
Ladybird species × photoperiod	$F = 18.01; P < 0.0001; df = 2, 239$	$F = 8.22; P < 0.0001; df = 2, 239$	$F = 1.42; P = 0.244; df = 2, 239$
Ladybird species × larval stage	$F = 1.37; P = 0.253; df = 3, 239$	$F = 33.97; P < 0.0001; df = 3, 239$	$F = 2.99; P = 0.032; df = 3, 239$
Photoperiod × larval stage	$F = 5.31; P < 0.0001; df = 6, 239$	$F = 10.29; P < 0.0001; df = 6, 239$	$F = 22.18; P < 0.0001; df = 6, 239$
Ladybird species × photoperiod × larval stage	$F = 2.74; P = 0.014; df = 6, 239$	$F = 6.45; P < 0.0001; df = 6, 239$	$F = 3.87; P = 0.001; df = 6, 239$

F-values significant ($P < 0.05$).

Further, the conversion efficiency differed significantly with ladybird species, larval stage, temperature and their interactions. However, the growth rate differed significantly with ladybird species, larval stage and temperature. Except the interaction between temperature and larval stage which was

insignificant, the other interactions between the independent factors were significant (Table 1). The conversion efficiencies and growth rates of larvae increased from 15 to 25°C , and thereafter decreased from 25 to 35°C ; being the highest at 25°C . At all temperatures, conversion efficiencies and growth rates

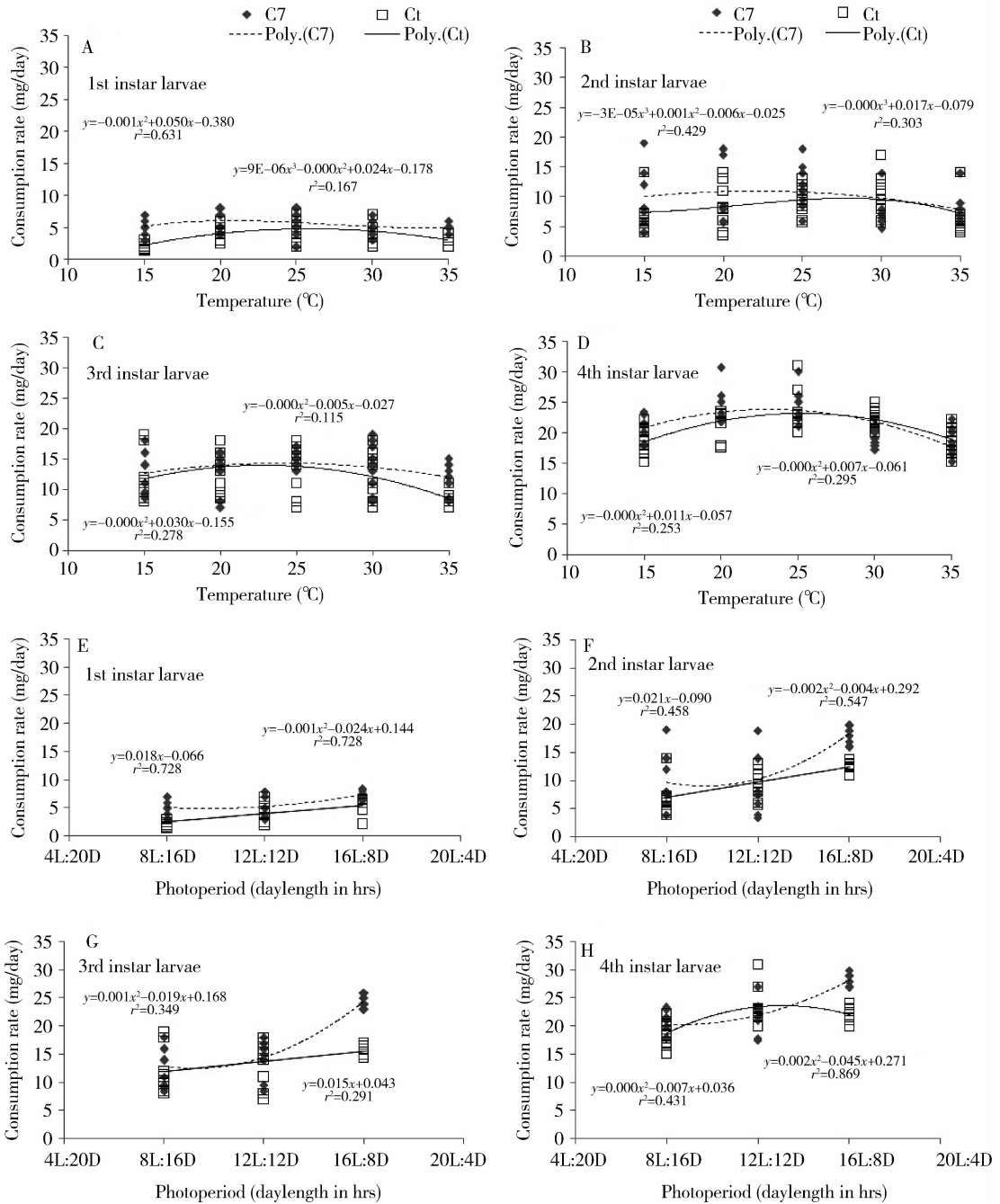


Fig. 1 Non-linear regression analysis showing the effect of different temperatures (A–D) and photoperiods (E–H) on consumption rate of larvae of *Coccinella septempunctata* (C7) and *Coccinella transversalis* (Ct)

Higher r^2 -values represent higher susceptibility to climatic cues.

were higher for early instar larvae and lower for the 4th instar larvae. Further the conversion efficiencies and growth rates were higher for *C. transversalis* and *C. septempunctata*, respectively (Table 2; Figs. 2–3).

Moreover, the biomass of newly emerged adults differed significantly with ladybird species and temperature, but not with their interaction (Table 3). Newly emerged adults of *C. septempunctata* and *C. transversalis* were the heaviest at 25°C and the lightest at 35°C (Fig. 4).

The lower magnitudes of r^2 -values of *C.*

septempunctata over r^2 -values of *C. transversalis*, when their larval consumption rates, conversion efficiencies and growth rates, and biomass of newly emerged adults were regressed against different temperatures, revealed the lower dependency of different temperatures to the larval predation rates of the former than to the latter (Figs. 1–3).

The developmental rate of larval stages was significantly influenced by the ladybird species and temperature. However, it did not differ significantly with the interaction between the ladybird species and

Table 2 Effect of temperature (T) on consumption rate, conversion efficiency and growth rate of larval instars of *Coccinella septempunctata* (C7) and *C. transversalis* (Ct)

T	Larval instars	Consumption rate (mg/d)	Conversion efficiency	Growth rate (mg/d)	T	Larval instars	Consumption rate (mg/d)	Conversion efficiency	Growth rate (mg/d)
15°C	1st instar	5.20 ± 0.49 aABβ	0.03 ± 0.01 aAα	0.48 ± 0.01 bBβ	15°C	1st instar	2.15 ± 0.19 aAα	0.15 ± 0.01 cBβ	0.36 ± 0.01 bAα
	2nd instar	9.68 ± 0.55 bBβ	0.09 ± 0.01 cCα	0.56 ± 0.02 dBβ		2nd instar	7.38 ± 0.16 bAα	0.08 ± 0.01 bAα	0.35 ± 0.01 bAα
	3rd instar	13.00 ± 1.05 cABα	0.09 ± 0.01 cBα	0.51 ± 0.02 cCβ		3rd instar	12.00 ± 1.16 cBα	0.17 ± 0.01 dAβ	0.42 ± 0.01 cAα
	4th instar	20.38 ± 0.73 dBβ	0.06 ± 0.01 bBα	0.12 ± 0.01 aBβ		4th instar	18.87 ± 0.70 dAα	0.03 ± 0.01 aAα	0.05 ± 0.01 aAα
20°C	1st instar	6.00 ± 0.49 aBβ	0.04 ± 0.01 aAα	0.53 ± 0.02 bCβ	20°C	1st instar	4.26 ± 0.33 aCα	0.20 ± 0.02 cCβ	0.41 ± 0.02 cBα
	2nd instar	11.47 ± 1.67 bBCβ	0.11 ± 0.01 dDα	0.64 ± 0.02 dCβ		2nd instar	8.68 ± 1.13 bBα	0.13v0.01 bBα	0.36 ± 0.01 bAα
	3rd instar	13.20 ± 1.00 bABα	0.08 ± 0.01 cBα	0.55 ± 0.02 cDβ		3rd instar	12.90 ± 1.04 cBα	0.19 ± 0.02 cBβ	0.45 ± 0.02 dBα
	4th instar	23.82 ± 0.88 cBCβ	0.06 ± 0.01 bBα	0.17 ± 0.01 aCβ		4th instar	20.83 ± 0.88 dBα	0.04 ± 0.01 aABα	0.06 ± 0.01 aABβ
C7 50°C	1st instar	6.00 ± 0.63 aBβ	0.06 ± 0.01 aBα	0.56 ± 0.01 bCβ	Ct 25°C	1st instar	4.75 ± 0.53 aCα	0.24 ± 0.02 cDβ	0.47 ± 0.02 cCα
	2nd instar	11.90 ± 0.80 bCβ	0.13 ± 0.01 cEα	0.73 ± 0.04 cDβ		2nd instar	9.12 ± 0.75 bBCα	0.17 ± 0.01 bDβ	0.38 ± 0.01 bABα
	3rd instar	14.80 ± 0.39 cBα	0.10 ± 0.01 bCα	0.56 ± 0.02 bDβ		3rd instar	13.90 ± 1.23 cCα	0.22 ± 0.01 cCβ	0.51 ± 0.02 dCα
	4th instar	24.73 ± 0.81 dCα	0.09 ± 0.01 bCα	0.24 ± 0.01 aDβ		4th instar	23.55 ± 1.00 dCα	0.05 ± 0.01 aBβ	0.07 ± 0.01 aBα
30°C	1st instar	5.00 ± 0.37 aAβ	0.03 ± 0.01 aAα	0.42 ± 0.01 bAα	30°C	1st instar	4.25 ± 0.44 aCα	0.21 ± 0.02 cCβ	0.44 ± 0.02 bCα
	2nd instar	7.94 ± 1.05 bAα	0.08 ± 0.01 cBα	0.51 ± 0.04 dAβ		2nd instar	9.92 ± 1.09 bCα	0.14 ± 0.01 bCβ	0.45 ± 0.02 bBα
	3rd instar	13.75 ± 1.19 cBα	0.06 ± 0.01 bAα	0.46 ± 0.01 cAα		3rd instar	12.50 ± 1.15 cBα	0.24 ± 0.02 dCβ	0.49 ± 0.02 cDα
	4th instar	19.70 ± 0.50 dABα	0.05 ± 0.01 bAα	0.14 ± 0.01 aBβ		4th instar	22.55 ± 0.43 dBcα	0.05 ± 0.01 aBα	0.08 ± 0.01 aBα
35°C	1st instar	5.00 ± 0.21 aAβ	0.03 ± 0.01 aAα	0.42 ± 0.01 bAβ	35°C	1st instar	3.10 ± 0.28 aBα	0.12 ± 0.01 cAβ	0.35 ± 0.01 bAα
	2nd instar	8.70 ± 0.92 bABα	0.06 ± 0.01 bAα	0.50 ± 0.02 dAβ		2nd instar	7.15 ± 1.18 bAα	0.06 ± 0.01 bBα	0.37 ± 0.01 bAα
	3rd instar	11.85 ± 0.73 cAβ	0.07 ± 0.01 bAα	0.47 ± 0.01 cBα		3rd instar	8.15 ± 0.38 cAα	0.16 ± 0.01 dAβ	0.44 ± 0.02 cAα
	4th instar	18.53 ± 0.70 dAα	0.04 ± 0.01 aAα	0.09 ± 0.01 aAβ		4th instar	18.53 ± 0.70 dAα	0.05 ± 0.01 aBα	0.05 ± 0.01 aAα

Values are mean ± SE; *F*-values significant (*P* < 0.05); small, large and Greek letters represent comparison of means among larval stages, among temperatures and between ladybird species, respectively.

Table 3 MANOVA table showing the effects of independent variables on dependent variables, viz., biomass of newly emerged adults and developmental rates of the immature stages of *Coccinella septempunctata* and *C. transversalis*

Independent variables	Temperature	
	Biomass of newly emerged adults	Developmental rate
Ladybird species	<i>F</i> = 809.28; <i>P</i> < 0.0001; <i>df</i> = 1, 99	<i>F</i> = 112.32; <i>P</i> < 0.0001; <i>df</i> = 1, 99
Temperature	<i>F</i> = 43.68; <i>P</i> < 0.0001; <i>df</i> = 4, 99	<i>F</i> = 172.56; <i>P</i> < 0.0001; <i>df</i> = 4, 99
Ladybird species × temperature	<i>F</i> = 1.70; <i>P</i> = 0.156; <i>df</i> = 4, 99	<i>F</i> = 1.12; <i>P</i> = 0.351; <i>df</i> = 4, 99

Independent variables	Photoperiod	
	Biomass of newly emerged adults	Developmental rate
Ladybird species	<i>F</i> = 36.81; <i>P</i> < 0.0001; <i>df</i> = 1, 59	<i>F</i> = 1.93; <i>P</i> = 0.170; <i>df</i> = 1, 59
Photoperiod	<i>F</i> = 42.25; <i>P</i> < 0.0001; <i>df</i> = 2, 59	<i>F</i> = 36.52; <i>P</i> < 0.0001; <i>df</i> = 2, 59
Ladybird species × photoperiod	<i>F</i> = 5.44; <i>P</i> = 0.007; <i>df</i> = 2, 59	<i>F</i> = 5.44; <i>P</i> = 0.007; <i>df</i> = 2, 59

F-values significant (*P* < 0.05).

the temperature (Table 3). The developmental rates of *C. septempunctata* and *C. transversalis* increased from 15 to 25°C and thereafter decreased with further increase in temperature; being higher for *C. transversalis* than *C. septempunctata*. The non-linear regression analysis (polynomial order three) fitted the data better than the linear regression analysis in the present study. The non-linear regression analysis revealed curvilinear incline in developmental rate from 15 to 25°C and thereafter a curvilinear decline in the rate of development from 25 to 35°C. The non-linear regression analysis further extrapolated ~ 11°C and ~ 10.5°C to be the lower development thresholds (LDT) and ~ 41°C and ~ 43°C to be the upper development thresholds for *C. transversalis* and *C. septempunctata*, respectively (Fig.4).

3. 2 Effect of photoperiod on predation and development of the immature stages of the two *Coccinella* species

MANOVA revealed significant influence of ladybird species, photoperiod and larval stage on the consumption rate of larvae. Except the interaction between ladybird species and larval stage which was insignificant, the other interactions between the independent factors were significant (Table 1). The consumption rate of larval stages increased from 8L: 16D to 16L: 8D. Under the three photoperiodic conditions, the consumption rates of both the ladybirds were the highest by the 4th instar larvae and the lowest by the 1st instar larvae; being higher for *C. septempunctata* than *C. transversalis* (Table 4; Fig. 1).

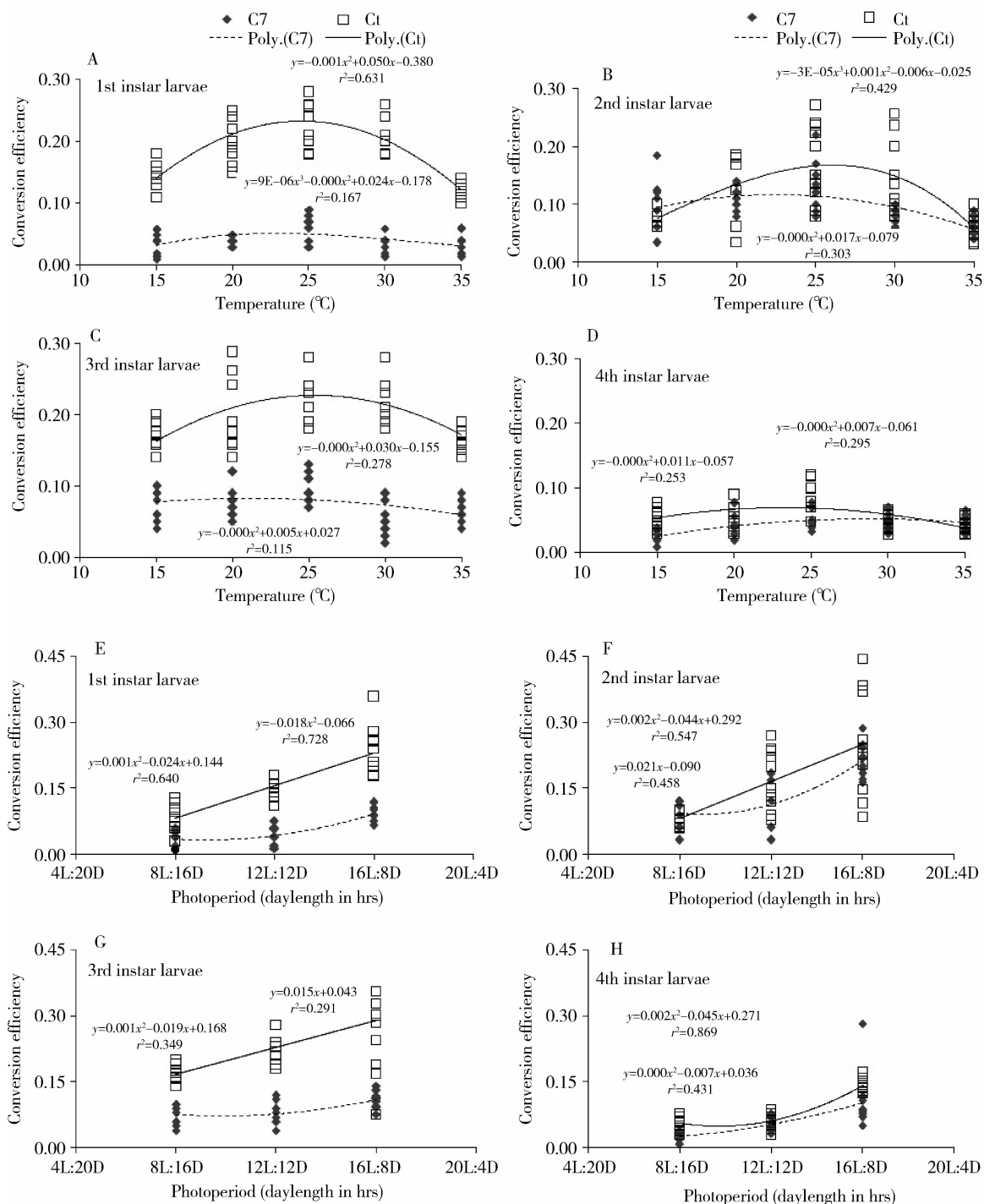


Fig. 2 Non-linear regression analysis showing the effect of different temperatures (A – D) and photoperiods (E – H) on conversion efficiency of larvae of *Coccinella septempunctata* (C7) and *C. transversalis* (Ct)

Higher r^2 -values represent higher susceptibility to climatic cues.

The conversion efficiency of larval instars was influenced significantly by the ladybird species, photoperiod, larval stage and their interactions. The growth rate of larval instars was influenced significantly by the ladybird species, photoperiod and larval stage. Except the interaction between ladybird species and photoperiod which was insignificant, the other interactions between the independent factors were

significant (Table 1). The conversion efficiency and growth rate of larval stages increased from 8L:16D to 16L:8D. Under three photoperiodic conditions, both the parameters were higher for early instars and lower for the 4th instar; being higher for *C. transversalis* than *C. septempunctata* (Table 4; Figs. 2–3).

The lower magnitudes of r^2 -values of *C. septempunctata* over r^2 -values of *C. transversalis*, when

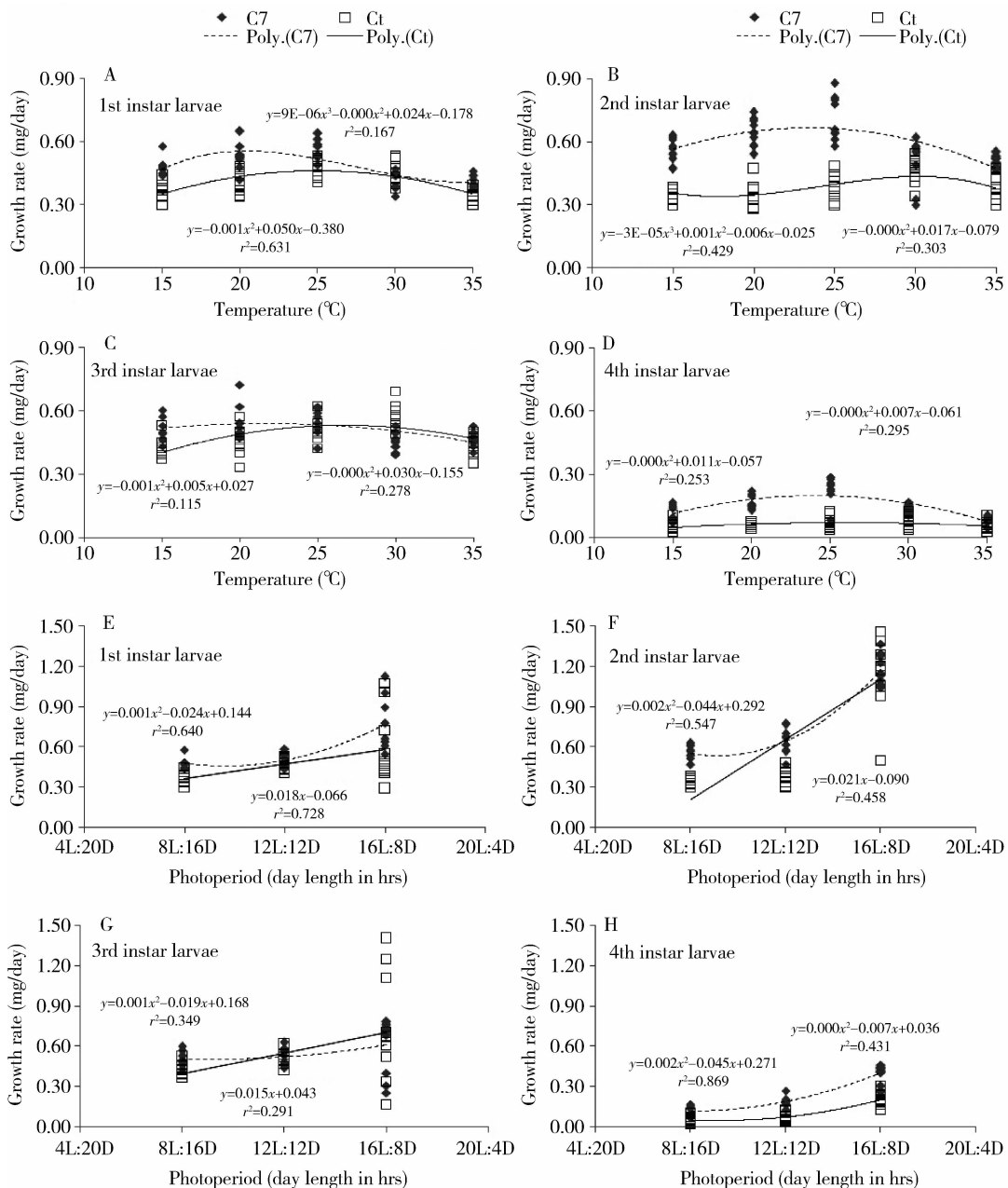


Fig. 3 Non-linear regression analysis showing the effect of different temperatures (A–D) and photoperiods (E–H) on growth rate of larvae of *Coccinella septempunctata* (C7) and *C. transversalis* (Ct)
Higher r^2 -values represent higher susceptibility to climatic cues.

their larval consumption rates, conversion efficiencies and growth rates were regressed against different photoperiods, revealed the lower dependency of different photoperiods to the larval predation rates of the former than to the latter (Figs. 1–3).

The biomass of newly emerged adults was influenced significantly by the ladybird species, photoperiod and their interaction. However, the developmental rates of the ladybirds at the immature stages differed significantly with the photoperiod and the interaction between ladybird species and photoperiod; but not with the ladybird species (Table 3). Newly emerged adults of *C. septempunctata* and

C. transversalis were the heaviest when larvae were reared at 16L:8D and lightest when reared at 8L:16D. Moreover, immature stages of *C. septempunctata* and *C. transversalis* developed the fastest at 16L:8D and slowest at 8L:16D (Table 4).

4 DISCUSSION

Increase in consumption rate, conversion efficiency and growth rate of *C. septempunctata* and *C. transversalis* larvae from 15 to 25°C and a decrease afterward from 25 to 35°C reveal that predation attributes of larvae increase with increase in temperature up to an optimum and thereafter decrease with further increase in temperature.

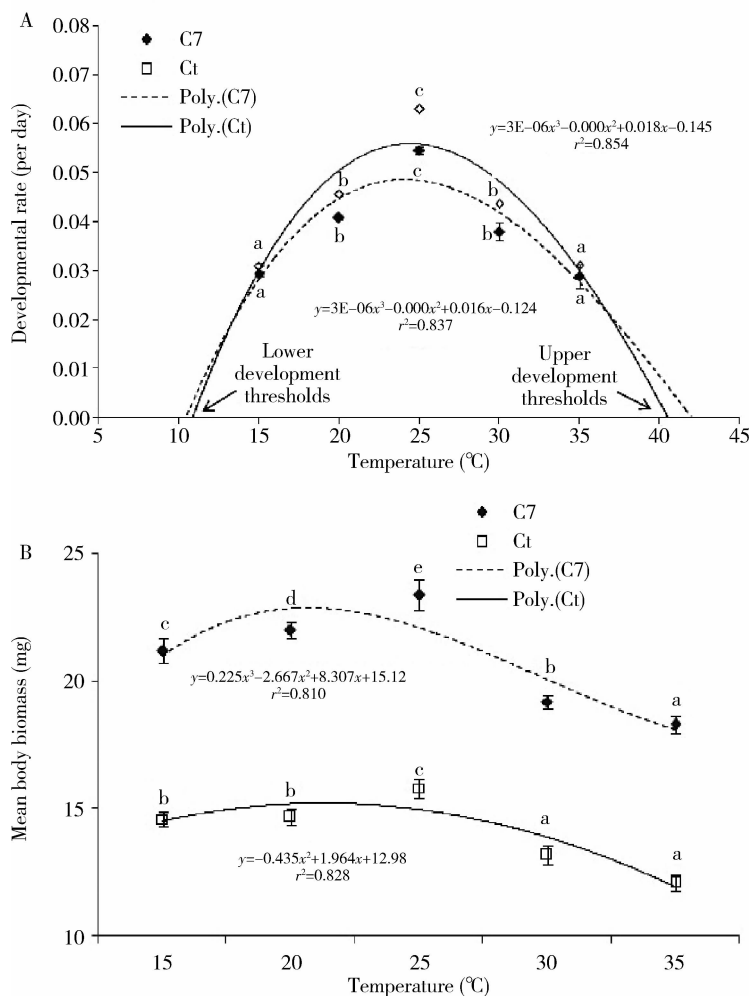


Fig. 4 Non-linear regression analysis showing the effect of different temperatures on the developmental rate of larvae (A), and the mean body biomass of newly emerged adults (B) of *Coccinella septempunctata* (C7) and *C. transversalis* (Ct)

Higher r^2 -values represent higher susceptibility to climatic cues; lower and upper development thresholds represent the extrapolated values of non-linear regression model; small letters represent comparison of developmental rates/mean body biomass among different temperatures.

At lower temperatures (15 and 20°C), the larvae are probably less active than those kept at optimum (25°C), and require less food to fulfill their low metabolic costs. Probably, the mobility of the prey species is also decreased when temperature is low, which further reduces their consumption by the predators. In contrast, optimum temperature accelerates the activities (prey searching and capturing, moulting to advanced stages, etc.) and metabolic costs of larvae that require high energy sources and the larvae consume, convert and utilize higher prey biomass to compensate for their high energy requirements and metabolic costs. The present results agree with earlier findings (Katsarou *et al.*, 2005; Manrique *et al.*, 2012). Moreover, higher temperature (30 and 35°C) possibly declines the activities of the predator and the prey species by inducing thermal stress (Khan and Khan, 2010; Sentis *et al.*, 2012; Yu *et al.*, 2014), and the larvae reared at higher temperatures probably consume and utilize less prey biomass than those kept at optimum (25°C).

Higher consumption rates, conversion efficiencies and growth rates of larvae of both the ladybirds at 16L:8D in the present study further reveal that the long photoperiodic condition probably facilitates foraging and higher prey exploitation by the ladybirds since they are diurnals, whereas exposure to short day length results in less prey consumption, conversion and utilization by the larvae (Omkar and Pathak, 2006; Berkvens *et al.*, 2008). Probably higher mobility of prey during long days also promotes its higher consumption by the ladybird predators. The results are in conformity with those reported in the western flower thrips, *Frankliniella occidentalis* (Pergande) (Whittaker and Kirk, 2004).

Amongst instars, maximum consumption of prey at all temperatures and photoperiods was recorded for the 4th instar larvae, possibly owing to their large size and high energy requirements needed for pupation. In contrast, higher conversion efficiency and growth rate of earlier instars over the 4th instar at all temperatures and photoperiods is probably due to their low energy

Table 4 Effect of photoperiod on consumption rate, conversion efficiency, growth rate of larval instars and newly emerged adults of *Coccinella septempunctata* and *C. transversalis*

Ladybird species	Photoperiod	Larval stage	Consumption rate (mg/d)	Conversion efficiency	Growth rate (mg/d)	Developmental rate (per day)	Mean body biomass of newly emerged adults (mg)
<i>C. septempunctata</i>	8L: 16D	1st instar	5.20 ± 0.49 aAβ	0.03 ± 0.01 aAα	0.48 ± 0.01 bAβ	0.068 ± 0.001 Aβ	21.90 ± 1.45 Aα
		2nd instar	9.68 ± 1.15 bAβ	0.09 ± 0.01 dAα	0.56 ± 0.02 dAβ		
		3rd instar	13.05 ± 1.05 cAβ	0.08 ± 0.01 cAα	0.51 ± 0.02 cAβ		
		4th instar	20.38 ± 0.73 dAβ	0.06 ± 0.01 bAβ	0.12 ± 0.01 aAβ		
	12L: 12D	1st instar	5.35 ± 0.43 aAβ	0.04 ± 0.01 aBα	0.50 ± 0.02 bBα	0.068 ± 0.001 Aα	23.40 ± 1.90 Aβ
		2nd instar	10.33 ± 0.73 bAβ	0.11 ± 0.02 dBα	0.65 ± 0.03 dBβ		
		3rd instar	14.60 ± 1.04 cAβ	0.08 ± 0.01 cAα	0.52 ± 0.02 cAα		
		4th instar	22.09 ± 0.89 dBβ	0.06 ± 0.01 bAα	0.19 ± 0.02 aBβ		
	16L: 8D	1st instar	7.44 ± 0.23 aBβ	0.09 ± 0.01 aCα	0.77 ± 0.06 cCβ	0.091 ± 0.002 Bβ	26.90 ± 1.20 Bβ
		2nd instar	18.50 ± 0.51 bBβ	0.21 ± 0.01 dCα	1.17 ± 0.04 dCα		
		3rd instar	24.50 ± 0.37 cBβ	0.11 ± 0.01 bBα	0.61 ± 0.16 bBα		
		4th instar	28.30 ± 0.33 dCβ	0.14 ± 0.01 cBβ	0.40 ± 0.02 aCβ		
<i>C. transversalis</i>	8L: 16D	1st instar	2.15 ± 0.19 aAα	0.09 ± 0.01 cAβ	0.36 ± 0.01 bAα	0.065 ± 0.001 Aα	20.30 ± 1.42 Aα
		2nd instar	7.38 ± 0.56 bAα	0.08 ± 0.01 bAα	0.35 ± 0.01 bAα		
		3rd instar	11.00 ± 0.54 cAα	0.17 ± 0.01 dAβ	0.42 ± 0.02 cAα		
		4th instar	18.87 ± 0.70 dAα	0.03 ± 0.01 aAα	0.05 ± 0.01 aAα		
	12L: 12D	1st instar	4.75 ± 0.53 aBα	0.15 ± 0.01 bBβ	0.47 ± 0.02 cBα	0.080 ± 0.002 ABβ	22.10 ± 0.29 ABα
		2nd instar	9.02 ± 0.55 bBα	0.17 ± 0.01 cBβ	0.38 ± 0.02 bAα		
		3rd instar	12.30 ± 1.03 cAα	0.22 ± 0.02 dBβ	0.51 ± 0.02 dBα		
		4th instar	17.13 ± 0.39 dBα	0.05 ± 0.01 aBα	0.07 ± 0.01 aBα		
	16L: 8D	1st instar	4.96 ± 0.55 aBα	0.24 ± 0.02 bCα	0.59 ± 0.08 bCα	0.090 ± 0.002 Bα	23.30 ± 0.82 Bα
		2nd instar	12.83 ± 0.24 bCα	0.25 ± 0.02 bcCβ	1.25 ± 0.12 cBα		
		3rd instar	15.58 ± 0.26 cBα	0.30 ± 0.04 cCβ	0.73 ± 0.13 bCα		
		4th instar	23.55 ± 1.00 dCα	0.10 ± 0.02 aCα	0.21 ± 0.02 aCα		

Values are mean ± SE; *F*-values significant ($P < 0.05$); small, large and Greek letters represent comparison of means among larval stages, among photoperiods, and between ladybird species, respectively.

requirements owing to their small size. Higher consumption rate of the 4th instar and higher conversion efficiency and growth rate of earlier instars have also been previously reported in ladybirds (Ahlawat *et al.*, 2008; Jalali *et al.*, 2009; Finlayson *et al.*, 2010; Mishra *et al.*, 2011, 2012; Kumar *et al.*, 2014a, 2014b).

In the present study, newly emerged adults of *C. septempunctata* and *C. transversalis* were the heaviest at 25°C, owing to highest prey consumption, conversion and utilization by the larvae at 25°C. However, the newly emerged adults at 35°C were lighter than those reared at 25°C, which may be attributed to poor prey consumption and utilization by the larval instars at 35°C than at 25°C. Decrease in body size with increase in temperature has previously been reported in insects (Kingsolver and Huey, 2008). Moreover, the biomass of newly emerged adults of both the ladybird species was more at 16L: 8D than at 12L: 12D and 8L: 16D. This may be ascribed to the tendency of ladybirds to consume more food under long day length conditions, as they are diurnal foragers. The results are in conformity with previous reports in insects (Chocorosqui and Panizzi, 2003; Amin and Kwon, 2011).

Increase in developmental rate (decrease in total

developmental duration) of larvae from 15 to 25°C may probably be due to increased consumption, conversion and utilization of prey biomass by the larval instars with increase in temperature. However, a decrease in developmental rate of larvae from 25 to 35°C is possibly a consequence of poor consumption and utilization of prey biomass. The increase in photoperiod further expedited the rate of development in both the ladybird species, probably owing to increased consumption rate, conversion efficiency and growth rate of larval instars with increase in day length. The results comply with the findings of previous studies in insects (Chocorosqui and Panizzi, 2003; Greenberg *et al.*, 2008; Berkvens *et al.*, 2008; Lopatina *et al.*, 2011). In contrast, continuous light had a negative effect on the physiology of the ladybird as reported in *P. dissecta* (Mishra and Omkar, 2005) and *H. axyridis* (Reznik and Vaghina, 2011).

In the present study, non-linear regression model predicted ~10.5°C and ~11°C as the estimated LDT value for *C. septempunctata* and *C. transversalis*, respectively, below which development of the respective ladybirds does not occur when fed on *A. pisum* and at 16L: 8D photoperiod and 65% ± 5% relative humidity. Earlier, Dixon *et al.* (2005)

reported 10°C as LDT for coccinellids. However, Katsarou *et al.* (2005) reported 10.7°C as LDT for *C. septempunctata*. Such slight variations in LDT may be owing to: (i) the effect of prey species (Jarosik *et al.*, 2014), and (ii) the different temperature ranges used in the study. Further, the non-linear regression model extrapolated ~41°C and ~43°C to be the upper development thresholds (UDT) for *C. transversalis* and *C. septempunctata*, respectively, above which the development probably ceases in both the ladybirds. It is likely that using a much wider range of temperature would greatly increase the accuracy with which LDT and UDT of ladybirds can be estimated.

Despite having similar size, the consumption, growth and developmental rates of *C. septempunctata* were higher (or similar in few cases) than *C. transversalis* at all temperatures/photoperiods. Also the former had lower larval predation and developmental rates dependency to temperature/photoperiod ($r_{CT}^2 < r_{CL}^2$; as revealed from regression analysis) than the latter. Probably, these and similar other intrinsic properties of *C. septempunctata* are associated with its dominance in most habitats of Palaearctic and Nearctic regions, as reported earlier by Hodek and Michaud (2008) and Omkar *et al.* (2014). A recent study has reported that weak photoperiodic responses facilitate the biological invasion of the harlequin ladybird *Harmonia axyridis* (Pallas) (Reznik *et al.*, 2015b). Thus, a ubiquitous ladybird species may be less susceptible to climatic cues and possibly has better adaptations to the local environment than the native species; since the former is associated with certain intrinsic advantages. Hence, the geographical range of distribution of the former is much wider than the latter.

In spite of having lower consumption rates, larvae of *C. transversalis* had higher conversion efficiency than those of *C. septempunctata* at all temperatures/photoperiods, so as to compensate for a shortage of food during their early phases of development. The results are in agreement with the findings of Kumar *et al.* (2014). In brief, the present study establishes a ubiquitous ladybird (*C. septempunctata*) as a better biocontrol agent of pea aphid over a native ladybird (*C. transversalis*) possibly owing to: (i) its higher consumption and growth rates at all temperatures and photoperiods, and (ii) its lower larval predation and developmental rates dependency to climatic cues. However, more field based studies are needed to further validate the present findings.

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温度和光周期对两种瓢虫捕食习性和发育的影响

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摘要:【目的】在农业上,气候变化影响作物产量、蚜虫动态以及捕食性瓢虫对蚜虫的调节作用。一些瓢虫为广布种,而另一些瓢虫种类却只在特定地理范围内分布,而有关气候因子如何影响瓢虫分布了解甚少。【方法】评价不同温度(15℃, 20℃, 25℃, 30℃和35℃)和光周期(8L:16D, 12L:12D和16L:8D)对两种瓢虫[七星瓢虫 *Coccinella septempunctata* (Linnaeus)(一种广布种)和狭臀瓢虫 *Coccinella transversalis* Fabricius(一种东方/南亚瓢虫)]幼虫取食和利用豌豆蚜 *Acyrtosiphon pisum* (Harris)的影响。【结果】尽管两种瓢虫的捕食作用和发育速率均在25℃时最高,但是随着日长的增加(即光周期从8L:16D增加到16L:8D)捕食作用进一步增强。与狭臀瓢虫相比,在所有温度和光周期下,七星瓢虫幼虫的取食量更高,生长和发育速率更快,其新羽化的成虫体重更重。非线性回归模型显示,七星瓢虫和狭臀瓢虫的最低发育温度分别为11℃和10.5℃左右,最高发育温度分别为41℃和43℃左右。狭臀瓢虫的幼虫捕食和发育速率对气候因子的依赖性强于七星瓢虫。【结论】本研究表明,广布种瓢虫对气候因子的敏感性比土著种瓢虫弱,因而可以广泛分布于不同的地理区域。因此,与土著种瓢虫相比,广布种瓢虫更适于作为生防因子。

关键词: 七星瓢虫; 狭臀瓢虫; 瓢虫; 温度; 光周期; 蚜虫

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